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Anolis jacare Boulenger, a "solitary" anole from the Andes of Venezuela

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ABSTRACT. *Anolis jacare* Boulenger is the sole member of its genus in the Andes of Mérida in Venezuela. In external morphology, size, and to some extent in behavior, it resembles its congeners on the one anole islands of the Lesser Antilles. The karyotype of *A. jacare*, however, demonstrates that it is not closely related to either of the two Lesser Antillean stocks which it resembles and these we know not to be closely related to each other. The similarity of *A. jacare* to the two Lesser Antillean stocks and of these to each other seems to be due to selection for a similar ecological type.

In 1903 Boulenger described *Anolis jacare* from several specimens in a collection made by S. Briceño at Mérida, Venezuela, at an elevation of 1600 meters. As all too frequently happens in Boulenger's work, the description was altogether without comparison or note on relationship.

Since its description additional specimens have been taken, all in the Venezuelan Andes, but there has been little discussion of the species. There has never been any question of its validity.

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Schmidt (1939: 9) mentioned a peculiar feature of the species, the double row of keeled scales forming the dorsal caudal margin. This is a feature which *A. jacare* shares with some South American species and with the very distantly related *A. barkeri* of Mexico. In 1960 Etheridge placed *jacare* in the *latifrons* series of his alpha section of the genus *Anolis*. This section, distinguished by the absence of transverse processes on the caudal vertebrae, represents an old endemic South American stock, which today shares South America with more recent (beta section) invaders from Central America.

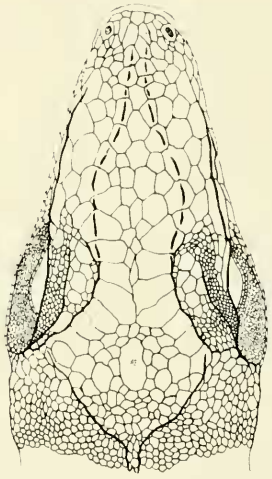

Figure 1. *Anolis jacare*. Dorsal view of head. AMNH 13444.

No previous mention of *A. jacare* has cited its most interesting feature: alone of native South American species, it shows a close resemblance to West Indian species, specifically those of the Lesser Antilles. In fact, its resemblance to *Anolis leachii*, except in size, is such that even an experienced student of *Anolis*, presented with a specimen of *jacare* without locality, is very likely to confuse it with *A. leachii*.

Table 1 compares *A. jacare* to *A. leachii* and to the Leeward Island species more similar in adult size, *A. marmoratus*.

When *A. jacare* is closely examined, of course, there should be no real possibility of confusing it with *A. leachii*. The dorsal squamation of the tail, larger dewlap, relatively larger ventrals, smaller scales on the snout, etc., permit easy recognition of *A.*

jacare. On general appearance, however, relationship will still seem plausible.

However, in terms of geography, close relationship of *jacare* of the Andes of Venezuela and *leachii* of the northern Lesser Antilles is *prima facie* unlikely. In addition, there is good evidence that the *bimaculatus* group (Gorman and Atkins, 1969) is derived from the still more distant Puerto Rican stock and that it is to this Puerto Rican stock or a still more primitive group that any phyletically meaningful resemblance would be expected.

Geographically, the *roquet* group in the southern Lesser Antilles would be a little more plausible as close relatives of *jacare* than the *bimaculatus* group. Gorman and Atkins (1969) have commented on the close external resemblance of the *roquet* and *bimaculatus* groups. Earlier, Underwood (1959) was able to find only the most trivial scale differences between the two groups. However, on all the characters by which Underwood was able to separate the *roquet* and *bimaculatus* groups, *jacare* fits the *bimaculatus* group.

With the eight Venezuelan species geographically closest, *jacare* shows little similarity. (None of the eight appear to overlap the distribution of *jacare* at all.) Five of the eight (*chrysolepis, auratus, fuscoauratus, tropidogaster, biporcatus*) belong to the beta division of Anolis (Etheridge, 1960) and are neither osteologically nor in squamation close to *jacare*. The three remaining species (*squamulatus, punctatus, tigrinus*) are referred by Etheridge (1960) to the same group as *jacare* (the *latifrons* series of the alpha section of *Anolis*). However, these again show no evidence of close relationship. *Squamulatus* and *tigrinus* are very different from *jacare* in size (*squamulatus* a giant, *tigrinus* a dwarf), and *punctatus* is conspicuously specialized in the swollen snout of the male. All differ significantly from *jacare* in scale characters.

There are indeed no South American or other continental species to which A. jacare *shows important resemblances.* We are left, therefore, with the external similarities to the *bimaculatus* species group and, less marked, to the *roquet* species group. If these resemblances go deeper, we appear to be faced with a zoogeographic puzzle which may need a difficult and complex solution.

It has seemed worthwhile, therefore, to broaden the study of *A. jacare* to include such more recently utilized characters as karyotype and ecology. The remainder of this paper deals with the results of these analyses.

Chromososome analysis (O. A. Reig and P. Kiblisky):

Four male and three female individuals have been worked for chromosome analysis. Our report is based on the four male individuals. We failed to get results with one of the females, and the other two were sent to Dr. George Gorman, who, by the use of a blood culture microtechnique, obtained a chromosome count agreeing with our results (personal communication). The male specimens have been deposited in the Collection of Herpetology of the Museum of Natural History of Caracas (MCNC 5601-5604). Those studied by Dr. George Gorman are in the Museum of Vertebrate Zoology, University of California.

Our animals were injected with 0.5 cc Colchicine Merck (solution 5 mg per cc) 2–3 hours before killing. Testes were removed, minced with scalpel, and pretreated for 20 minutes in a hypotonic solution of sodium citrate 0.7%. The material was centrifuged at 800 rpm and the pellet resuspended in 3/1 alcohol-acetic fixative. After a new centrifugation, the pellet was changed to 2/1 fixative. Spreads were obtained by air-drying on chilled slides or by squashing, then stained with acetolactic orcein, Giemsa and Feulgen, and mounted in Canadian balsam. Chromosomes were observed with a Wild M-20 microscope, and each appropriate metaphase or meiotic prophase was recorded and sketched. Numerous additional cells were also counted and observed. Selected cells from those recorded were photographed with high contrast Copy Kodak film, and karyotypes were constructed from enlarged prints. A total of 50 cells was recorded, as listed below:

	Spermatogonial metaphases	*Diakineses*	*Metaphases II*
Specimen Nr. MCNC 5601	9	3	—
Specimen Nr. MCNC 5602	4	1	1
Specimen Nr. MCNC 5603	15	1	—
Specimen Nr. MCNC 5604	13	3	—
All specimens	41	8	1

Results

The diploid chromosome complement of *Anolis jacare* is composed of 32 chromosomes (Figs. 3 and 4). Of them, 12 are macrochromosomes and 20 are microchromosomes. The diakineses (Fig. 5) show six large bivalents and ten very small bivalents. Chromosome number and structure are identical in all the studied specimens. The six pairs of macrochromosomes do not gradually

decrease in size but can be divided into three groups (Fig. 1). Group A is formed by three pairs of large metacentric and submetacentric chromosomes. (In the following, we use the nomenclature proposed by Levan, Fregda, and Sandberg, 1964.) Pair A-1 comprises *sm* chromosomes, whereas pairs A-2 and A-3 are *m*-chromosomes. Chromosomes of pair B-1 are around 4/5 the length of those of pair A-3. Pairs B-1 and B-2 are easily distinguishable in size. Group C comprises one pair of small *st* chromosomes ($r = 3.66$), clearly smaller than those of pair B-2 and three times larger than the largest chromosome of the set of the microchromosomes. A small difference in size and arm ratio was found in the chromosomes of this pair in all the cells where the shape of these chromosomes was clear enough, so that the pair might tentatively be considered as heteromorphic. Whether or not the presumptive heteromorphic pair is to be interpreted as an X-Y sexual system cannot be solved in the absence of good female metaphases. In two of the chromosome spreads obtained by Gorman, the female karyotype also shows heteromorphism in this pair. Moreover, the ring-shaped form of the corresponding bivalent in male diakinesis does not seem to fit with the X-Y hypothesis. The 20 pairs of microchromosomes steadily decrease in size and seem to have terminal (*t*) or subterminal (*st*) centromeres.

Gorman (1965), Gorman and Atkins (1967, 1968a) and Gorman, Atkins and Holzinger (1967) have demonstrated that a karyotype of six pairs of macrochromosomes and twelve pairs of microchromosomes is shared by most of the studied species of iguanid lizards, including the anoles of the alpha group of Etheridge (1960) other than those of the *bimaculatus* series. The anoles of the beta group of Etheridge depart from this "standard" iguanid karyotype in showing seven pairs of macrochromosomes and a variable number of microchromosomes. Within the alpha group, the species of the *bimaculatus* series known in chromosome constitution (*bimaculatus, leachii, gingivinus,* and *marmoratus*) (see Gorman, 1965; Gorman and Atkins, 1966) are peculiar in having quite another kind of karyotype. In these species there is no sharp distinction between macro- and microchromosomes. There are from 18 to 20 chromosomes gradually decreasing in size that continue in five or six pairs of dotlike microchromosomes.

Anolis jacare departs from both the beta anoles and alpha anoles of the *bimaculatus* series in retaining the "standard" set of six pairs of macrochromosomes, easily distinguishable from the

microchromosome set. The morphological similarities referred to above with members of the *binaculatus* series are thus not supported by chromosome evidence, but this evidence agrees with the osteological evidence in indicating that this species belongs to the alpha group. Within the non-*binaculatus* series alpha anoles so far known in chromosome structure, however, a considerable variation occurs in details of structure of the macrochromosome set and in the number of microchromosomes. *Anolis roquet, equestris, carolinensis,* and *cybotes* are different from *Anolis jacare* in showing 22 or 24 microchromosomes and a steady decrease in size of the macrochromosomes, the only distinguishable break in size in these being between the fifth and the sixth pairs. *Anolis cooki, pulchellus, cristatellus* and *scriptus* of the *cristatellus* series (Gorman, Thomas, and Atkins, 1968) show the two sharp breaks in the macrochromosomes that are also observed in *A. jacare,* but in them the second break falls between the fourth and the fifth pairs instead of between the fifth and the sixth pairs as in *A. jacare.* In addition, those species of the *cristatellus* series mentioned above have heteromorphic sex chromosomes and only from 15 to 18 microchromosomes. *A. trinitatis* and *A. aeneus* of the primitive *latifrons* series agree with *A. jacare* in the two size discontinuities among the macrochromosomes. They have, however, 24 and 22 microchromosomes respectively, and the first break in the macrochromosomes falls between the second and the third pair. Moreover, the first pair of macrochromosomes is metacentric in all the illustrated karyotypes of alpha anoles, whereas it is submetacentric in *A. jacare.*

Anolis jacare thus seems to be an isolated species within the alpha group on the basis of the pattern of the size discontinuities among the macrochromosomes and the unique number of 20 microchromosomes. It is suggestive that a distinction of three groups within the macrochromosomes falling in the same order as in *A. jacare* can also be observed in the species of the beta anoles of the *grahami* and *chrysolepis* series so far reported (Gorman, 1965; Gorman and Atkins, 1967). There is, however, a sharp difference between the macrochromosome set of these species and that of *A. jacare*: in the former the group C comprises two pairs instead of one pair as in the latter, the number of pairs of macrochromosomes thus amounting to a total of seven, as in all of the beta anoles.

Given the widespread occurrence of six pairs of macrochromosomes in alpha anoles and most iguanids, we are inclined to evaluate differences in number of the macrochromosome set as more important than structural rearrangements within this portion of the karyotype. For this reason, and because *A. jacare* is clearly an alpha *Anolis* on osteological grounds, the similarities it shows with some of the beta anoles in chromosome structure are better interpreted as a departure from the "standard" iguanid karyotype that converged with some of the modifications shown in the anoles of the *grahami* and *chrysolepis* series. Admittedly, the amount of this convergence may be considerable. It would be possible to derive the karyotype of *A. jacare* from that of *A. chrysolepis* by centromeric fissions in the last pair of macrochromosomes of the latter, leading to two pairs of microchromosomes with terminal centromeres. This process would result in a complement with six pairs of macrochromosomes separable into three distinct groups, and in ten pairs of microchromosomes, exactly as in *A. jacare*. The osteological evidence, however, does not support any close relationships between these two species.

The chromosome analysis thus indicates that *Anolis jacare* is an alpha *Anolis* that has departed significantly from other members of this group in chromosome number and structure, though maintaining the standard iguanid karyotypic feature of six pairs of macrochromosomes.

Observations in life (C. Rivero-Blanco and E. E. Williams):

Since no information of any ecological sort had ever been provided for *Anolis jacare,* it was as important an objective of the expedition to Mérida to provide this information as to obtain chromosome data.

Only twelve anoles were collected during a period of three days of active search. All were obtained on medium and large-sized trees bordering the small Rio Milla just outside the city of Mérida (1639 meters above sea level). Several other areas within and outside the city of Mérida were carefully examined.

The general area is classified as Premontane Humid Forest in the scheme of L. R. Holdridge (J. J. Ewel and A. Madriz, 1968). The mean annual temperature is 19.1° C and the annual rainfall 1791 mm.

The two actual collection sites (Fig. 2) were roadside localities and were subject to more or less penetration by the sun, especially so in site 1 where trees were partly separated, less so in site 2 where the canopy was closed. In the first site, the anoles were

seen and collected on the branches of "majagua" (*Heliocarpus popoyensis,* Tiliaceae) and "guamo" (*Inga* sp., Leguminosae), at the second on "anime" (*Montanea quadrangularis,* Compositae) and on a very large tree 10–15 meters high, not identified, since leaves and flowers were not collected.

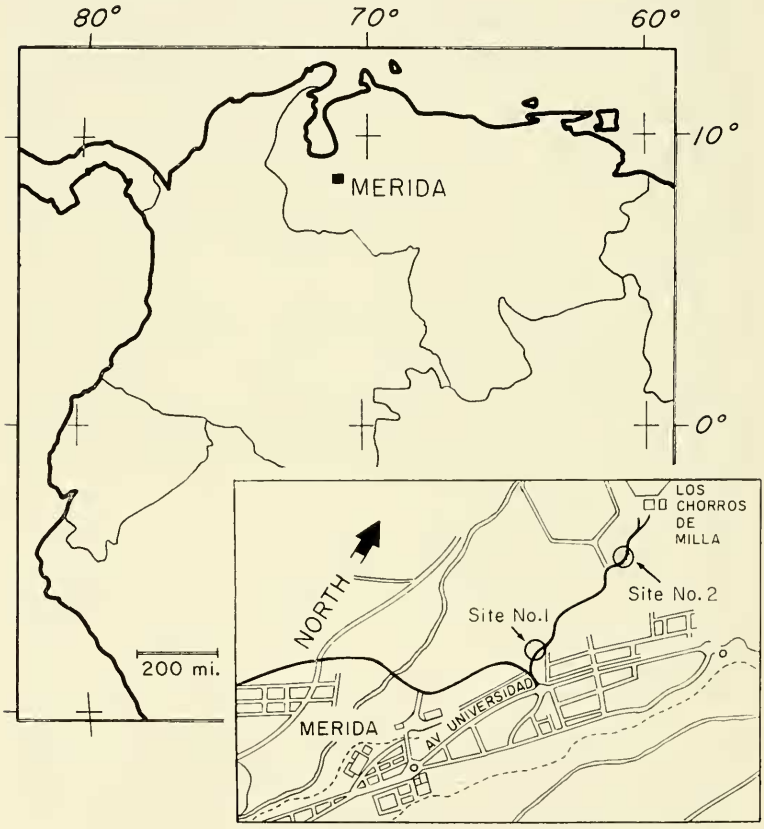

Figure 2. Map of the collecting sites for *Anolis jacare* along the Rio Milla outside Mérida.

Collecting was done with the aid of a 5 meter long telescopic fishing rod with a nylon noose. The animals were not shy but avoided the noose by moving around the branch or further along the branch or to other branches along the trunk or out on the finer twigs. Two escaped high into the canopy; others did not move at

all. The number of animals seen varied from none on many trees to four on one guamo tree. Few of those seen escaped the noose.

We have no belief that we have even the beginning of knowledge of the population density of this species. The animals were difficult to see and commonly lay along branches, and only twice were they seen on the main trunk of the trees. They obviously ranged widely within the trees they inhabited, including very high in the crown. The first specimen taken came from a guamo tree that was examined several times every day and even one night. It was this tree that, on the last afternoon, provided three additional animals to give a final result of two males and two females on a tree no more than six meters high and not especially complex. This result was possible only because, during the last afternoon, we had the help of a young local boy who was an excellent climber and who was able to spot from a higher position animals that could not be seen from below because of their resting position on branches.

In summary, this is an animal inhabiting primarily the crown and its branches, though not avoiding the trunk. It is not restricted to shade; several individuals seen were in partial sun or moved into sun without reluctance. It has no evident competitors. No other lizards were seen in the collecting area either on the trees or on the ground. Elsewhere in the vicinity other lizards were found: *Polychrus,* in a hedge, and *Ameiva* and *Cnemidophorus,* on the ground.

Discussion (E. E. Williams):

The karyotypic evidence clearly demonstrates a strong separation between *jacare* and either of the stocks of Lesser Antillean anoles. Equally there is sharp difference between *jacare* and the few mainland alphas that have been studied thus far (Gorman, personal communication). On the face of the evidence, *A. jacare* seems to occupy a rather isolated phyletic position.

It may be of interest and importance here that *A. jacare* is distributionally isolated also and that, very unusually for South American anoles, it is not known to be sympatric with any congeners in any part of its known range.

There are other South American species that extend beyond the range of their congeners somewhere at the periphery of their range. *A. jacare* is special in that so far as known its whole range is outside contact with any other anole.

Recent studies by T. Schoener (1970) have shown that in the Lesser Antilles, "solitary" species, i.e., species without sympatric

congeners, tend to be very similar in size and habitus. There also appears to be a broadened unspecialized ecology characteristic of these "solitary" anoles. We have noted above that the *bimaculatus* and *roquet* species groups are extraordinarily similar in scale characters. We emphasize now that they are so in spite of the fact that they are products of two quite separate invasions of the West Indies and are very distinct in karyotype and biochemistry.

Schoener infers, and we may agree with him, that some common selective factor must be at work to keep (or evolve) external similarity when wide underlying differences exist. That common selective factor would appear to be the negative one of the absence, or extreme limitation, of the number of congeners.

Certainly on the larger islands of the Greater Antilles a contrary rule exists: syntopic anoles are very diverse in morphology or size or both.

The modification of a species in the absence of congeners or other competitors in its general niche is sometimes spoken of as "release." In morphology, at least, it is proper to speak of a more positive selection than that implied by that essentially negative term. A certain size seems clearly optimal and presumably the features of squamation must likewise be held under selective control.

In ecological behavior, "release" seems a more descriptive term, since the wider range of habitat permitted a species in the absence of close competitors concords better with our intuitive sense of the meaning of release.

In the Lesser Antilles, there is often only one species per island and, except for instances of very recent importation and their very local occurrence (e.g., *wattsi* on St. Lucia, Underwood, 1959, 1962), there is a maximum of two species per island. These are relatively old islands and the species on them are well differentiated. They afford the classic and best examples of "solitary" anoles.

A. jacare, however, is as isolated in the Andes of Mérida as the solitary anoles of the Lesser Antillean islands. It is effectively on a mainland island; it is interesting therefore, but not unexpected, however, to find it resembling and behaving like an island anole—a solitary anole of an old small island.

The resemblances, then, of *A. jacare* to *A. leachii* or *A. marmoratus* are to be explained in terms of adaptation to similar selective pressures. We need not, in fact, seek any complex zoogeographic solution to the similarity of one anole on island mountains

to one on a distant island; the similarity is non-phyletic, strictly convergent.

TABLE 1

	jacare	*leachii*	*marmoratus*
snout-vent length of adult ♂	73 mm	96 mm	77 mm
scales across snout	6-8	4-5	4-5
scales between semicircles	0-2	0-1	0-1
loreal rows	4-5	4-5	4-5
scales between interparietal and semi-circles	1-3	1-2	1-2
supralabials to center of eye	6-9	7-8	7-8
mental	*not* deeper than wide	*not* deeper than wide	deeper than wide
number of sublabials in contact with infralabials	3-5	2-4	2-4
scales between sublabials in contact with mentals	4	4-6	3-4
ventrals	smooth	smooth	feebly keeled
lamellae under phalanges ii and iii of fourth toe	19-25	26-32	24-30
tail	compressed but without crest, 2 dorsal rows	compressed, with strong crest in males	Compressed, with weak dorsal crest in males
dewlap	large	small	large
color	green with variable dark vermiculations	green with dark vermiculations but these stronger on head than on body	green with light vermiculations on head in males only

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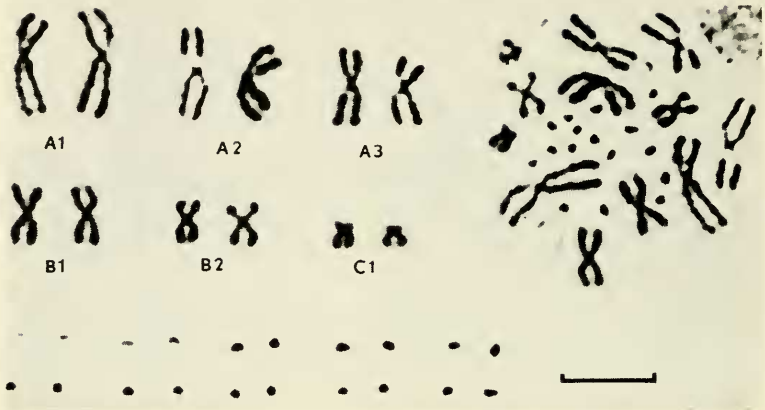

Figure 3. Spermatogonial metaphase and karyotype of *Anolis jacare*. Specimen no. MCNC 5601, cell no. A-167 T5 C2. Scale: 10 micra.

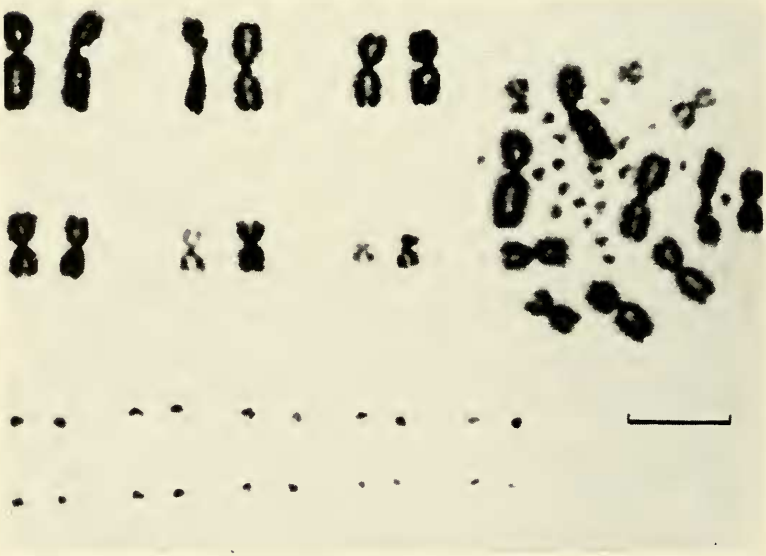

Figure 4. Spermatogonial metaphase and karyotype of *Anolis jacare*. Specimen no. MCNC 5604, cell no. A-171 T3 C2. Scale: 10 micra.

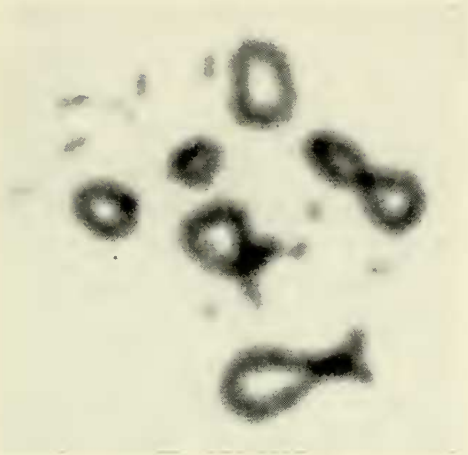

Figure 5. Diakinesis of *Anolis jacare*. Specimen no. MCNC 5603, cell no. A-170 T7 C1.

Figure 6. Rio Milla, Merida (site 1 of Fig. 2). To the right of the light post is the guamo (*Inga* sp.) in which two males and two females were collected. The other trees to the right are majagua (*Heliocarpus popayensis*) where other specimens were collected